

ANALYSIS

Is the Tasmanian tiger extinct? A biological–economic re-evaluation

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Abstract

In the 1890s, a bounty scheme was implemented to rid Tasmania of the thylacine or Tasmanian tiger, a marsupial predator believed to wreak havoc on imported sheep flocks. The thylacine is now officially ‘possibly extinct’ and although, repeatedly, there have been alleged sightings in the wild, most people now believe the species is extinct as there has been no confirmed evidence of its survival over the last 70 years. We develop a bioeconomic model to re-evaluate the likelihood that thylacines are alive today, or whether the turn of the last century demand for dead tigers drove the species to extinction. Our results suggest the bounty did not drive thylacines to extinction.

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1. Introduction

The last Tasmanian tiger (*Thylacinus cynocephalus*) in captivity died in Beaumaris Zoo, Tasmania, on September 7, 1936. Although there have been hundreds of alleged sightings of Tasmanian tigers, or thylacines, in the wild since 1936, no one has established the existence of a living individual beyond reasonable doubt. Numerous

studies have looked for the tiger, including those sponsored by the World Wide Fund for Nature, and those spurred by a \$100 000 reward offered by billionaire Ted Turner and a \$250 000 reward offered by tourist entrepreneur Peter Wright. Despite the considerable effort expended searching for this marsupial wolf-like predator and the hundreds of unsubstantiated sightings, no clear photographs have been taken, no unambiguous footprints have been found, and no dead tigers have turned up as road kill along roads crossing the tiger’s habitat (see [Park, 1985](#); [Quammen, 1996](#); [Guiler and Godard, 1998](#); [Paddle, 2000](#)).

Such curiosity fueled by the mysterious sightings has turned the Tasmanian tiger into a mythical

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species whose existence remains hotly debated today—similar but different from some others like the monster of Loch Ness, Bigfoot, or the Yeti. Unlike these others, we know that the tiger existed for certain. In fact, the species was once so common in Tasmania that it was considered a nuisance, leading both private entrepreneurs and public policy-makers to put a price on its head.

Why? Consider the historical reason for the bounty. Tasmania is a 68 000-km² island that lies 240 km south of the Australian continent. The first Europeans arrived in 1803 and began exploring and developing part of the country—displacing the society of Aborigines who must have arrived at least 40 000 years ago. The advent of Europeans, and especially the introduction of new farm animals such as sheep, had a profound influence on conditions for the thylacine. By the 1830s, the sheep industry was well-established, and investors started complaining about severe livestock losses. Although Guiler and Godard (1998) and Paddle (2000) demonstrate that predation by tigers must have been a relatively minor concern to the grazing industry compared to theft, predation by wild dogs, bad farming practices and losses due to inhospitable living conditions, tigers were known to kill sheep and were considered a major pest.

In 1840, the private Van Diemen Land Company introduced a bounty system for tigers caught on the properties under its control. Eventually, pressures from the grazing industry led to government involvement. In November 1886, the parliament offered £1 for every adult tiger brought in and 10 shillings for each young tiger. A dead tiger was worth about a week's wages, and this incentive proved hard to resist. The predominant way of killing a thylacine was through inexpensive neck-snares. This allowed people to enter freely into the tiger hunting business. The persecution of the species began in earnest. A European demand for its pelt added to the tiger's bad luck. Both, the demand for the bounty and the pelts caused a significant decline in the species' abundance.

The official status of the thylacine is now 'possibly extinct' (King, 1988), but fewer and fewer people actually believe the species persists (Guiler and Godard, 1998; Paddle, 2000; Bowman, 2001). If thylacines still exist in Tasmania, several

factors complicate their search. The most likely habitat is sizeable and inhospitable, with many natural barriers. This makes the range covered by search teams at any one time relatively small. Also, the area is largely undeveloped, decreasing the probability of chance encounters. Thylacines are also shy and nocturnal, making observation even more difficult. Finally, normal densities of the territorial thylacines are sparse, with a range of about 50–75 km per pair. Yet despite these challenges, many researchers are still fascinated about the possible existence of the thylacine.

Herein we step back and re-evaluate the likelihood that the turn-of-the-century demand for dead tigers drove the species to extinction. As suggested by Bowman (2001) and consistent with other recent studies of extinction (e.g. the Pleistocene megafauna collapse, studied by Alroy (2001)), we explore the dynamics of the tiger population by combining biological elements and economic behavior into a single mathematical model. We develop an open access hunting model that simulates harvest levels and abundance of thylacines and human hunters over time, accounting for a wide range of possible parameter values. Our results indicate that economic forces could not have led to the species' demise, and support the view that tigers could still exist in the wilds of Tasmania today. We estimate that a significant wild population existed until the 1920s, and abundance might have been sufficient to ensure enduring survival. Unless some unknown disaster struck this extant population in the interim, our findings suggest that hunting tigers for bounty and pelts should not have triggered the ultimate demise of the population.

2. A bioeconomic model of hunters and tigers

We recreate the dynamics of the Tasmanian tiger population by developing a bioeconomic model.¹ Good economic and biological data are

¹ See Paddle (2000) and Guiler (1985) for discussions on interesting but somewhat different cause of thylacine extermination on the Australian mainland.

difficult to secure. We know that thousands of animals were killed in the late 19th and early 20th century, but many important statistics have been lost. We know exactly how many thylacines were presented annually for government bounty between the bounty period of 1888 and 1908, but it also clear that such numbers do not tell us how many tigers were actually harvested.

As argued by Guiler and Godard (1998, p. 128): ‘...the records do not represent the real number of total kills. Many trappers have said that up to half the tigers snared were not submitted for bounty but were carted around and offered to local property owners who paid a reward (usually £1). When the carcass became too smelly it was dumped in the bush. The number of thylacines killed and disposed of in this manner is a complete mystery.’ Because the official government bounty has, for some unknown reason, stimulated property owners and firms to pay a similar bounty for every dead tiger, the official statistics are (potentially gross) underestimates of the true number of tigers killed annually and should not be used to assess the species viability. Park (1985, p. 124) supports this observation: ‘One tannery in Tasmania exported 3482 skins to London between 1878 and 1896. At least 4800 of the animals were killed between 1878 and 1909, an appalling rate of attrition for such a rare species.’

As a word of caution, the number of animals presented for bounty (2184) and sold for their pelts (3482 until 1896) should not be added because the bounty set is likely a subset of the pelts sold. A trapper would take a carcass to the nearest police station, where the claim was typically paid. The toes were then clipped off or the ears were removed so that it could not be presented for bounty again (Guiler and Godard, 1998). But presumably many trappers would then sell the altered carcass to a tannery.

Our observations on ‘hunting effort’ over time are also incomplete, but we do know the number of men that collected government bounty each year. With respect to the biological side, Guiler and Godard (1998, p. 17) argue, ‘pathetically little is known.’ Both growth and abundance information leave much to be desired.

We specify an integrated biological and economic model (see, for example Wilen, 1976; Conrad and Bjørndal, 1991; Amundsen et al., 1995), and examine the consequences of the data imperfections by applying a broad range of parameter values. First, consider the economic component, which is in the tradition of Smith (1968). Harvests are defined according to the conventional Schaefer harvest function $h = qEx$, where h is the number of tigers caught, x is the tiger population (measured in animals), q is the catchability coefficient, and E is hunting effort—the number of people who annually hunted for tigers.² Property rights for tigers were undefined; everybody could potentially enter the snaring business. Consistent with standard open access models, assume E is increased when the associated financial returns exceed the returns to alternative occupations, i.e., agriculture. Assuming unskilled labor earns a fixed amount w per day working in agriculture, the dynamics of hunting effort are³

$$E_{t+1} - E_t = v\pi_t = v(BqE_t x_t - wE_t) \quad (1)$$

where v is a parameter representing the speed of entry into or exit out of the snaring business, and π_t is defined as the *profits* of tiger killing at time t , or the return to catching tigers minus the opportunity costs—agricultural income foregone. In Eq. (1), B is the sum of the bounty paid per dead tiger and the value of the animal’s pelt.

For the biological component, we postulate a lumped parameter growth function and assume that growth of the thylacine population occurs according to

$$\begin{aligned} x_{t+1} - x_t &= G(x_t) - h_t \\ &= rx_t(1 - (x_t/k)) - \alpha - qE_t x_t, \end{aligned} \quad (2)$$

where population growth $G(x)$, is a logistic growth process augmented with a shift parameter (α) to

² A more realistic measure would be a combination of the number of trappers, the number of traps, and the number of days per week that the traps are checked. However, such data are, unfortunately, not available.

³ Eq. (1) represents a myopic decision rule for entry and exit and is consistent with most economic models of open access. An alternative, but also more complex, approach would involve rational expectations (Berck and Perloff, 1984).

incorporate a minimum viable population. The intrinsic growth rate is given by r . In conventional models, k is the population's carrying capacity. Here, the parameter α shifts the logistic growth function down. Graphically, this implies that $G(x)$ intersects the horizontal axis twice at positive stock levels; $G(x) = 0$ for $0 < x_1^* < x_2^* < k$, where x_1^* is the minimum viable population (MVP) and x_2^* is the carrying capacity:⁴

$$x_1^* = \frac{r - \sqrt{r^2 - (4r\alpha/k)}}{2r/k} \quad \text{and} \\ x_2^* = \frac{r + \sqrt{r^2 - (4r\alpha/k)}}{2r/k}.$$

This growth representation allows for extinction along an equilibrium path when hunting is sufficiently profitable.⁵

In [Appendix A](#), we calibrate a benchmark scenario for the system of difference [Eqs. \(1\) and \(2\)](#). Due to a lack of data, we apply two further assumptions that would only have the effect of biasing the model towards extinction. First, we do not distinguish between adult and juvenile animals, and assume that the bounty for adult animals (£1) applies for all harvested tigers. Second, we do not model any 'safe havens' for the tiger to retreat in the model. Obviously, if tigers do presently live in Tasmania, they must do so in a safe haven. But incorporating this explicitly in a deterministic model would ensure that at least a small population survives. Instead, we incorporate spatial issues indirectly by modeling a gradual reduction in thylacine carrying capacity over time such that eventually less than 30% of the carrying capacity remains. Any animals that might still exist would do so in a much smaller habitat range. This is in line with the idea that agricultural

development and associated reduction in availability of herbivore prey may be an important factor explaining the demise of the thylacine.

3. Did the bounty scheme drive the tiger to extinction?

3.1. The benchmark scenario

[Eqs. \(1\) and \(2\)](#) are used to obtain the dynamics of hunting effort, harvest levels and tiger populations. [Fig. 1](#) shows the time paths for the benchmark scenario. The quantitative results reported in [Fig. 1](#) are roughly consistent with available data on tiger hunting effort and harvest levels as reported by [Guiler and Godard \(1998, Tables 7.2 and 7.3\)](#).

The bounty system triggered substantial entry by hunters in early periods resulting in a large decline in tiger abundance, followed by a decline in the number of hunters. The hunter population is at its maximum in 1903–1904 when 0 profits are earned. Harvest levels also increase rapidly, level off, and then collapse after the turn of the century. The model estimates that 'peak' harvesting occurred in 1895, or some 4 years earlier than in the official statistics. The reported harvest levels are consistently greater than the number of thylacines presented annually for government bounty, which is consistent with the fact that many killed thylacines were presented to private parties, not the government statistics office. The cumulative harvest from 1888 to 1908 is 3773 tigers, or 1.7 the number of times that bounty was paid (2184 times, see [Appendix A](#)), which coincides nicely with the statement by [Guiler and Godard \(1998\)](#) that 'up to half the tigers snared were not submitted for bounty'. The simulated cumulative harvest of 3773 thylacines is also consistent with [Park \(1985\)](#) estimate of 4800 killings from 1878 until 1909. Recall that Park's time frame is ten years longer than our simulated time frame (which starts in 1888). If we use any of the harvest paths from [Fig. 1](#) (our simulated output or the government bounty data) and extrapolate backwards in time we would easily account for the difference of 1027 tigers (or 4800–3773).

⁴ Note that $\alpha < rk/4$ to avoid imaginary solutions (i.e. the growth function should not be shifted down too much to retain the results of two distinct solutions to $G(x) = 0$).

⁵ Without critical depensation, extinction will only occur as hunters overshoot the equilibrium in the first cycle of a spiral approach path. Under such models, extinction only occurs when hunters are earning losses as costs go to infinity as the stock goes to 0. With instantaneous exit, extinction will not occur in a model without critical depensation ([Clark, 1990](#)).

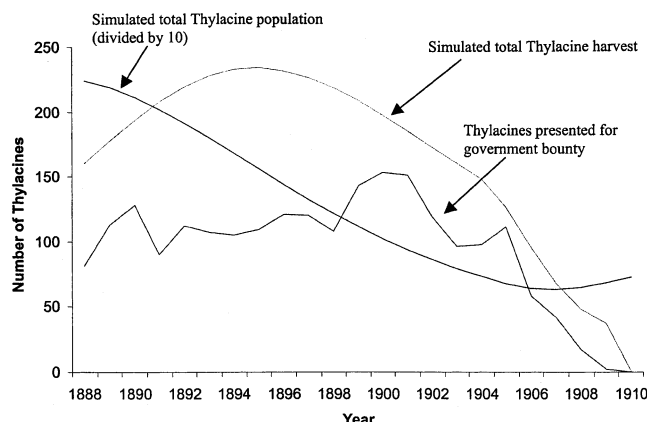


Fig. 1. Baseline model predictions vs. thylacines presented to the government for bounty.

The most important result evident from Fig. 1 is that the tiger population was in no danger of extinction. Our numerical model estimates an ‘all time low’ level of abundance of about 632 tigers (in 1907), which eventually increases to a steady-state level of 779 animals (assuming the carrying capacity stops diminishing around this time) after hunting ceases.⁶ Because, unlike for effort and harvest, there are no reliable population estimates available for the early 20th century, it is impossible to hold this number up to a ‘reality check.’ To explore the robustness of the survival result, we run the numerical model 5000 times while randomly varying the parameter values (including initial effort and harvest levels)—a Monte Carlo simulation. Appendix A presents the parameter ranges considered.

3.2. A Monte Carlo simulation and the likelihood of species survival

Figs. 2 and 3 provide the results from the Monte Carlo analysis in which we randomly draw parameter values from uniform distributions with

bounds that range from 75 to 125% of the benchmark values (see Appendix A). Fig. 2 summarizes the distribution of simulated ‘all time low’ tiger stocks. Typically, such lows were reached a few years before the bounty scheme ceased in 1909, when hunting for scarce tigers became unprofitable and hunters began to exit the industry. This allowed the thylacine population to recover somewhat. Fig. 3 gives the distribution of simulated cumulative tiger harvests for the period 1888–1908, further suggesting that a majority of the carcasses were never handed in for government bounty.

How do the numerical results in Figs. 2 and 3 bode for the medium- to long-term survival of the species? Considering the distribution of minimum stock levels (the ‘all time low’ numbers reported in Fig. 2), we find that 100% of the probability mass is to the right of the MVP level of 50 animals. Conservation biologists argue that populations of more than 500 animals are likely to maintain sufficient genetic diversity and the long-term ability to respond to changing circumstances (Primack, 1998; Soulé, 1987). We find that 68% of the probability mass is to the right of the 500-animals threshold. If we increase the MVP to 100 animals and redo the Monte Carlo analysis, we find that thylacine extinction is the result in only two cases out of 5000 runs. Again, this indicates that extinction is possible but very unlikely. These results suggest that the chances are good that a

⁶ Paddle (2000) indicates that indirect human predation on tigers occurred as hunters who were searching for kangaroos, etc. set out poison to kill tigers that might have eaten prey from their snares. We simulated this additional mortality effect by multiplying harvests by a factor greater than one. Surprisingly, this only helped conserve the tigers—as their population diminished faster, hunters’ profits fell and they exited earlier.

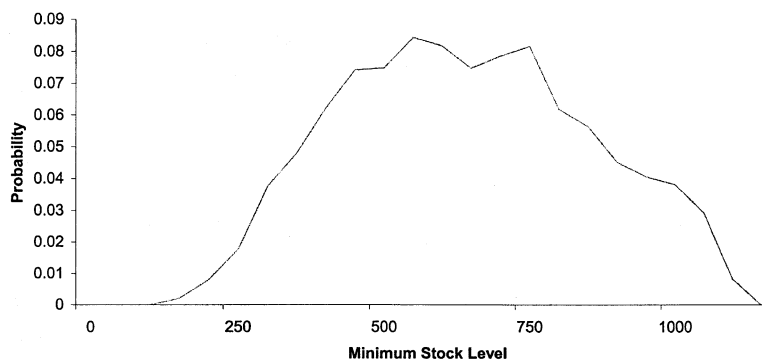


Fig. 2. Simulated distribution of minimum stock levels: 1888–1920.

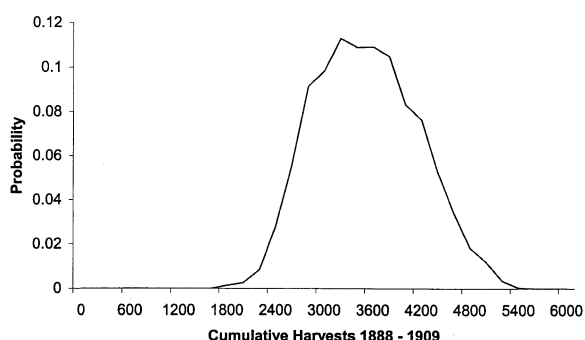


Fig. 3. Simulated distribution of cumulative harvests 1888–1909.

viable population of Tasmanian tigers existed after the bounty scheme was aborted.

Finally, even if the bounty scheme had continued, we predict it would not have enticed sufficient hunting effort to kill off the entire population. A much greater bounty (equal to £5.1) would have been required to cause extinction due to over-harvesting.⁷ With such a bounty in place, sufficient hunting effort would be lured into the snaring business in early periods so that tigers would have been harvested below the MVP level. Harvesting ends prior to extinction, but the population cannot recover. For comparison, the amount of £5.1

equaled more than a month of wages for unskilled labor, an unlikely amount even if the goal was to eliminate a tiger.

4. Conclusion and discussion

Did the Tasmanian government drive the thylacine to extinction with its bounty scheme intended to protect sheep? In addition, if the answer could be ‘no,’ is there a chance that the species is still surviving in a remote part of its initial habitat? Our results suggest the answer to the first question is ‘no.’ A considerable population of tigers most likely existed in 1909 when the bounty scheme was terminated, and chances are that population was sufficiently abundant to ensure the continued survival of the species. This finding suggests that a viable population could possibly exist at near-carrying capacity level in the periphery of its initial habitat. This is presumably what a density-dependent spatial migration model would predict. The low density, the shyness of the animals, and their nocturnal habits would prevent frequent encounters between these predators and humans. Similarly, some of the hundreds of unconfirmed thylacine sightings may have been correct as individual animals spill out of their habitat onto nearby fields or land (former tiger habitat).

Our results also counter the basis for the hypothesis that a ‘distemper-like disease’ might have ravaged the populations of thylacines in 1908 (McCallum and Dobson, 1995; Guiler and Godard, 1998; Daszak et al., 2000). Although ‘hard

⁷ Alternatively, a 78.5% reduction in the labor wage rate (to £0.75) in 1888 and later years, given the existing bounty scheme in place, could have led to extinction. Of course, if the wage fell in later years, for example after the bounty had been reduced, then a much more significant wage reduction would have been needed to result in extinction.

evidence remains absent' (McCallum and Dobson 1995, p. 191), alleged support for this hypothesis is the fact that financial returns to hunting suddenly dropped after 1906 which, it is argued, would not have happened with overharvesting. Our numerical results, however, show that this sudden drop in financial returns is *exactly* what happens with overharvesting.

While there is some evidence that a 'distemper-like' disease did exist, there is controversy over whether it was fatal (McCallum and Dobson, 1995; Guiler and Godard, 1998) or merely debilitating (Paddle, 2000). Even if an incredibly lethal disease did strike after most harvesting ceased and wiped out, say, 50% of the tiger population, it is unlikely that the species would go extinct in the short run. Assuming an exogenous 50% population crash in abundance in 1908, 100% of the distribution's probability mass is in excess of 50 individuals, 90% is in excess of 250 animals, but no more than 15% of the simulation runs indicate populations is in excess of 500 animals. The combination of bounty hunting and a disease might have compromised the long run (but not the short term) viability of the species.

Exterminating the thylacine a century ago was equally difficult and costly as exterminating current 'pest species' (Quammen, 1996). Bowman (2001), for example, notes that Australian land managers using modern technologies such as helicopters and military assault rifles are incapable of exterminating current nuisance species such as feral pigs, buffaloes and donkeys. When prey densities fall, hunting returns drop too and in response, effort moves out. This reemployment of effort reduces the pressure on the hunted species, presumably allowing it to recover—as did the Australian Saltwater crocodile (*Crocodylus porosus*) and the New Zealand fur seal (*Arctocephalus forsteri*) when hunting pressure was removed.

A key caveat applies to our results. A spatial model would be useful for a broader understanding of the dynamics and recovery of the thylacine population. Without spatial data or knowledge of migratory movements in response to relative densities, developing a spatial metapopulation is not feasible (but see Sanchirico and Wilen (1999) for a theoretical model). The effect of developing a

spatial model with several subpopulations on extinction probabilities is likely ambiguous. While small populations may be more vulnerable to stochastic shocks (Soulé, 1987), it is also likely that some of these small populations are located in remote areas, virtually unaffected by hunting pressure. Such 'safe havens' may play an important role in species survival. For example, recent work by Channel and Lomolino (2000) suggests that many species are likely to survive in the periphery of its historical range, consistent with the remote and uninhabited regions of Tasmania where tigers may still exist.

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Appendix A: Model Calibration and Monte Carlo Analysis

Model Calibration

For the deterministic baseline numerical model, we adopt the following parameter values: (1) the price of a dead tiger, $B = £1.6$, or the sum of £1 (bounty) and £0.6 (pelt) until 1909 and £0.6 thereafter (Guiler and Godard, 1998; GG hereafter). (2) The opportunity cost of labor, $w = £3.5$. We base this on the assumption that wages for unskilled labor are £1 per week (GG), and that an individual spends one day a week setting and checking snares for approximately 6 months a year (the winter season). (3) The parameter α is chosen such that the MVP equals 50 animals. Evidence suggests that wildlife populations of fewer than 50 animals run a considerable risk of going extinct due to the vagaries of nature within a 100 year period (Primack, 1998). (4) GG estimate Tasmania's carrying capacity for thylacines to lie between 2000 and 4000 animals, or a maximum of one pair of tigers per 50–60 km². We adopt an initial value

of 2800, such that $k = 2850$ ($k = x_2^* + \text{MVP}$ due to symmetry of the quadratic growth function). There is a 3% annual decline in the species' carrying capacity, which corresponds to more than a 70% decline by 1930. (5) Tanner (1975) reports intrinsic growth rates of similar wild populations (in terms of size and weight, litter size, etc. For example, wolves, lynx, and mountain lion) lie between 20 and 40%. We use the value $r = 0.25$. (6) The 1888 population of thylacines is assumed to be $x_0 = \phi x_2$, where $\phi = 0.8$ for the benchmark. (7) 1888 effort levels are estimated at 25 hunters based on estimates by GG. (8) 1888 harvest levels are not readily available. We use the value of 160, which is somewhat larger than the number of claims for government bounty (GG). (9) The catchability coefficient, q , is calibrated using the Schaefer function and initial effort levels, population levels, and harvests. (10) Data on entry and exit parameters are obviously lacking. We ran the model repeatedly using the above-mentioned parameters, while varying the exit and entry parameters to reproduce the reported harvesting and effort data as closely as possible (i.e. to mimic the qualitative pattern of rise and fall in harvesting over time, and to 'scale' simulated output to approximate known output). We find that the simulated results best conform to the data when two different values were chosen for v : one value for the speed of entry into the snaring business, v_1 (when $\pi > 0$) and another for the speed at which hunters exit, v_2 (when $\pi < 0$). When using a symmetric entry/exit rate ($v_1 = v_2$), we find that

either extinction occurs before 1900 or there is continued harvesting after 1910. We chose the values $v_1 = 0.02$ and $v_2 = 0.5$. We note that the results are rather sensitive with respect to these parameter values. Notably, increasing v_1 or decreasing v_2 would increase the odds of extinction. But increasing (decreasing) v_1 (v_2) also implies that harvests cannot be supported into the year 1910. This leads us to reject such values.

Monte Carlo Analysis

We recognize the challenge of uncertainty about the baseline parameter values. We address this challenge by performing a Monte Carlo analysis in which the model is run 5000 times using randomly drawn combinations of parameter values. We assume each parameter is uniformly and independently distributed according to reasonable bounds. A combination of parameter values is then randomly chosen for use in the simulation. This procedure is repeated 5000 times so that each instance of the simulation represents a probable state of the world. The result is a distribution of outcomes that allow us to assess the robustness of the model. Table A1 shows the distributions of parameter values.

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Table A1
Parameter distributions

Parameter	Benchmark value (mean)	Distribution ^a
w	3.5	$U(2.625, 4.375)$
x_2	2800	$U(2100, 3500)$
r	0.25	$U(0.1875, 0.3125)$
ϕ	0.8	$U(0.6, 1)$
E_0	25	$U(18.75, 31.25)$
h_0	160	$U(120, 200)$
v_1	0.02	$U(0.015, 0.025)$
v_2	0.5	$U(0.375, 0.625)$
MVP	50	$U(37.5, 62.5)$

^a Each distribution is uniform with the bounds being 25% higher and 25% lower than the mean.

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